AGE-RELATED CHANGES IN MOVEMENT PATTERNS IN THE FISHING SPIDER, *DOLOMEDES TRITON* (ARANEAE, PISAURIDAE)

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ABSTRACT. Based on the pattern of movement used during the search for prey, predators can generally be placed into one of two categories: active or passive searchers. This study documents an age-related switch in the movement pattern of the pisaurid spider *Dolomedes triton*. Individual spiders were marked and followed during two consecutive seasons on two ponds at the Patuxent Wildlife Research Center in Laurel, Maryland. Mean distances moved per day were compared between adult females and juveniles. During both years, and on both ponds, adult females traveled significantly greater distances per day than did juveniles (1.88 ± 0.33 m *vs.* 0.19 ± 0.02 m for adult females and juveniles, respectively; years and ponds pooled). This shift suggests an age-related difference in foraging strategy. Repeated observations on individual female spiders support the notion that juvenile *D. triton* switch to a more active search mode upon maturation. It is hypothesized that this change in movement represents a switch in foraging strategy in response to increased energy requirements during yolk production.

It is generally regarded that predators search for prey by using one of two basic modes. "Ambush" searchers (Greene 1983; Gerritsen & Strickler 1977), also known as "sit-and-wait predators" (Huey & Pianka 1981; Pianka 1966) or "passive searchers" (Eckhardt 1979), remain stationary for long periods of time, waiting for prey to enter their field of perception. They contrast with animals that move continuously through the environment; these are known as "cruise predators" (Greene 1983; Gerritson & Strickler 1977), "widely foraging predators" (Huey & Pianka 1981; Pianka 1966), or "active searchers" (Eckhardt 1979). Web-building spiders have been offered as the exemplary sit-and-wait predator (Riechert & Luczak 1982). However, spiders differ in their residence times at a web-site, both within and between species. Prey availability and hunger have been implicated in the selection of, and tenacity at, foraging sites for many spiders (e.g., Turnbull 1964; Riechert & Tracy 1975; Gillespie 1981; Janetos 1982a, 1982b; Morse & Fritz 1982; Olive 1982; see Wise 1993 for a review). Two models attempting to explain this relationship have been developed and applied to web-building spiders: 1) Janetos' (1982a) adaptation of a patch-selection model from optimal foraging theory and 2) Caraco and Gillespie's (1986; Gillespie & Caraco 1987) risk sensitivity model.

The general spider models of Janetos and Caraco & Gillespie may not apply to many cursorial spiders. While crab spiders which hunt from discrete inflorescences are particularly amenable to analysis with patch-selection models of optimal foraging theory (e.g., Morse 1986, 1988; Morse & Fritz 1982, 1987), it may be difficult to apply this approach to spiders that do not use a discrete, well-defined site. Definitions of "site" and measurement of "site quality" are difficult when the boundaries themselves are ambiguous. Risk-sensitive models of movement assume that in a given habitat, the two strategies of active and passive foraging yield the same expected total number of prey but differ in

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their variance. This may be the case for a web forager, which builds a web and then must wait for prey to enter. However, rapid movement by wandering spiders may result in increased encounters with prey, perhaps by leading to additional types of prey in the diet (Huey & Pianka 1981; DeVita et al. 1982). This may result in differences in the means as well as the variances of the prey expected under each of the two strategies.

The lack of appropriate models or formal analyses of the foraging behavior of spiders that do not capture prey with webs is likely related to the general lack of substantial data. Few studies have rigorously examined movement and foraging modes among the cursorial spiders. Riechert & Luczak (1982) argue that cursorial spiders primarily employ a sit-and-wait strategy in foraging for food because of the need to conserve energy. They hypothesize that natural selection has favored individuals which minimize energy expenditure. Thus, even salticids, which are generally considered to be very active foragers, spend much of their time stationary on a substrate and orient to prey only when it enters the visual field of perception (Givens 1978).

Comparing different age classes of the same species may be a fruitful approach to understanding the environmental correlates of different foraging behaviors in spiders, since much of the confounding variation present in interspecific comparisons is absent. Researchers have seldom made clear distinctions between the possibly different selective constraints on foraging for prey of juvenile and adult spiders (with the exception of males, which switch to foraging for females upon maturation). Such distinctions may be important. An extreme example is the pisaurid *Pisaura mirabilis* Clerck in which juveniles use a prey-catching web, but adults actively hunt (Lenler-Eriksen 1969). Similar behavior has been attributed to species of the tetragnathid *Pachynatha* Sundevall (Gertsch 1979).

In this paper we report the discovery of a marked age-related change in the movement pattern of an entirely cursorial species, the fishing spider *Dolomedes triton* Walckenaer. We document the switch of juvenile females to a more active mode that occurs upon reaching sexual maturity, and then introduce the hypothesis that this ontogenetic change in behavior represents a switch in foraging strategy

in response to increased energy requirements during yolk production.

METHODS

Biology of *D. triton*.—*D. triton* is a very large (body length: 0.9–2.5 cm) member of the family Pisauridae that occupies the shorelines of ponds and lakes throughout North America. Spiders of the genus *Dolomedes* Latreille, the most aquatic of the pisaurids, are able to run on and dive under the water surface in order to catch prey and escape predation. *D. triton* is a generalist predator, utilizing a wide prey spectrum. Rather than using webs, displacement of the water surface is used to detect and locate prey (Bleckmann & Barth 1984). Foraging is closely associated with vegetation. These spiders are typically observed resting on emergent vegetation with at least one leg contacting the water surface (Carico 1973; Bleckmann & Rovner 1984; pers. obs.). Vegetative sites provide not only a resting site during foraging, but also the support necessary for breaking surface tension during dives for predator avoidance (McAlister 1960).

Invertebrates active near or on the surface of the water are most likely to be taken as prey by *D. triton* (Zimmerman & Spence 1989). Prey items commonly are other pond predators, such as gerrids, notonectids, and odonates. Vertebrates such as tadpoles and small fish are sometimes eaten as well (Bleckmann & Lotz 1987). Additionally, Zimmerman & Spence (1989) report that all instars except the smallest juveniles and adult males are cannibalistic, feeding on conspecifics of smaller or similar size.

D. triton takes two years to reach sexual maturity (Carico 1973). Adults can be found between May and September in central Alberta, Canada (Zimmerman & Spence 1989, 1992) and between April and November in Maryland, USA (pers. obs.). Juvenile *D. triton* overwinter among debris and vegetation close to the margins of ponds and lakes (Bishop 1924; Kaston 1948). Zimmerman & Spence (1989, 1992) report that overwintering juveniles reinvade the water surface as soon as the ice melts, when they commence feeding and reach the adult stage after an additional 2–3 molts.

Study area.—The spiders were observed on two artificial freshwater ponds located in

the Patuxent Wildlife Research Center in Laurel, Maryland. Bluegill Pond is approximately 150 m × 45 m with an average depth of about 1.1 m. Marginal vegetation primarily consists of *Sparganium americanum* (burreed), *Eleocharis quadrangulata* (square-stem spikerush), *Scirpus cyperinus* (woolgrass), *Juncus effusus* (softrush), *Nuphar luteum* (spatterdock), *Nymphaea odorata* (white waterlily), *Polygonum hydropiperoides* (swamp smartweed), and two large stands of *Saururus cernuus* (lizardtail). Farm Pond is approximately 60 m × 60 m, with an average depth of 2 m. Principal marginal vegetation consists of *Eleocharis quadrangulata, Potamogeton diversifolius* (pondweed), *Liquidambar styraciflua* (sweetgum), *Polygonum hydropiperoides* and *Juncus effusus*.

In 1991, 35 m of the north margin of Bluegill Pond were partitioned into 1 m² quadrats by staking with bamboo poles. In June 1992, the south and east margins of Farm Pond were similarly demarcated. Maps displaying the features of the ponds' perimeters, including vegetation, were created and used to identify and record locations of *D. triton*.

Data collection and analysis.—The partitioned area of Bluegill Pond was searched for spiders at least three times per week from 11 July–15 October 1991 and from 23 April–29 June 1992. In July 1992 the dam on this pond broke and the pond was almost completely drained. Consequently, the study was moved to Farm Pond and continued from 12 July–3 November 1992.

Searching involved slowly wading around the perimeter of the ponds or paddling in a rubber boat. The location of each spider sighted was recorded on a map. Other information, such as the activity of the spider, the vegetation it was touching, and its posture in relation to that vegetation, was also recorded. Some spiders were captured, measured, and their carapace marked with Liquitex® acrylic paint for identification. Marks were applied with a thin paintbrush using the 1–2–4 marking code described by Zimmerman & Spence (1982). Marked spiders were returned to the same site from which they were taken. This approach provided both a cross-sectional sample of habitat use by the population and longitudinal mark-recapture data on a portion of the population. Spiders were remarked with the same identifying number following a molt only if

the spider was found in close proximity to the exoskeleton and displayed the characteristic greenish cast of a newly molted individual (Zimmerman & Spence 1982; pers. obs.). Additionally, missing and regrown appendages were used to assist identification.

When marked spiders were resighted, the mean distance moved per day was conservatively calculated by assuming that spiders moved in a straight line from the previously sampled point, and then dividing by the number of days since the last sighting. Additionally, the distances of each resighting from the point of the initial sighting were calculated as an estimate of the range of movement. These methods of measurement only indirectly reflect activity levels, but in the absence of continuous monitoring, provide an approximation of movement. Although all age and sex classes were marked, adult males were excluded from the analyses. Adult male *D. triton* are rarely found feeding (Zimmerman & Spence 1989) and their movements probably reflect mating rather than feeding activities.

RESULTS

During both years, and on both ponds, adult females traveled *ca.* 10 times farther per day than did juveniles (Table 1). Juveniles and adult females also differed markedly in their total range of movement, estimated for resighted spiders as the distance from the first sighting (Fig. 1). Early in the season, only juveniles were present on the pond, and very little movement was evident. During the midseason, when juveniles and adults coexist, the contrast between the two age classes was dramatic. Juveniles continued to move very little while females were considerably more active. In late fall, after the adults had died, increased movement by juveniles was observed. This is likely to be due to overwintering activity, rather than foraging, since these spiders were often found on the shore itself under dried vegetation. Farm Pond was also equipped with an overflow drain, which created a directional flow of water during wet periods. This flow may have affected juvenile movement as well. The fall movement was not observed the previous year on Bluegill Pond.

Although adult females are generally larger than juveniles, the increased movement is not strictly associated with the adults' larger size (Fig. 2). The largest juveniles do not move

Table 1.—Mean meters moved per day by juvenile and adult female *Dolomedes triton* without egg-sacs. In order to make the analyses from the two ponds comparable, only the data collected between 1 July and 31 October were analyzed. *T*-tests adjusted for unequal variances were used to compare the mean distances for juvenile and adult females.

		n	Mean distance (m)	SE	P
1991 Bluegill pond	Juveniles	7	0.10	0.02	
	Adult females	24	1.83	0.52	0.003
1992 Farm pond	Juveniles	59	0.20	0.02	
	Adult females	16	1.94	0.28	0.0001

significantly more than small juveniles, despite a carapace width that is indistinguishable from adult females. Likewise, adult females with small carapace widths do not move less than those with large carapaces. Maturity, rather than carapace width, predicts the mean distance moved (MANOVA, $P < 0.05$).

The behavioral change in movement pattern is correlated with the occurrence of the last molt (Figs. 3–6). Before molting, penultimate females exhibited the typical juvenile pattern of movement. Following molting, a sharp increase in movement occurred. The increase in activity did not simply take place within a home range, as indicated by the distance moved from first sighting. The spiders moved considerably until the egg sac was constructed. Once the egg sac was formed, females moved much less and resumed a pattern characteristic of juveniles. The mean distance moved per day by females with egg sacs was 0.19 ± 0.03 m ($n = 18$; 1991 observations in Bluegill Pond). In contrast with juveniles, females with egg sacs were never observed feeding. Egg sacs were continuously held in the chelicerae until hatching.

Thirty-two nursery webs were examined at Bluegill Pond in 1991. Forty-seven percent of
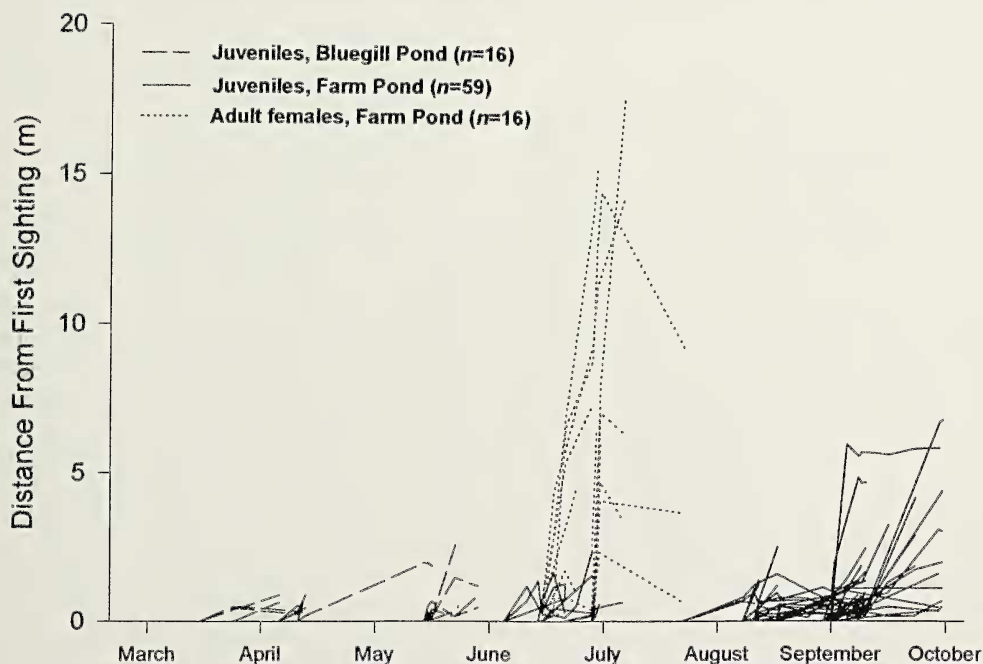

Figure 1.—Distances moved from the first sighting of juvenile and adult female *Dolomedes triton* in 1992 during the early season on Bluegill Pond and mid-late season on Farm Pond.
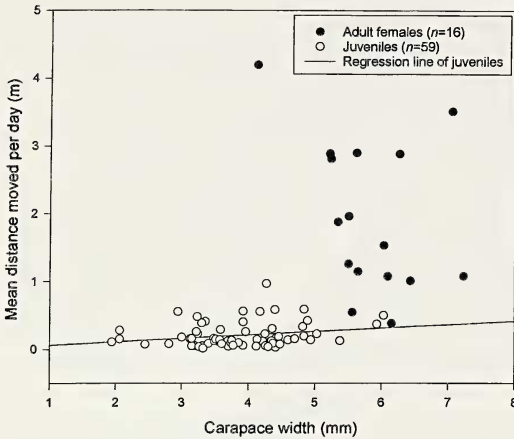
Figure 2.—Mean distances moved per day in meters as a function of carapace width for both juvenile and adult female *Dolomedes triton* without egg sacs. The regression line of the juveniles is shown.

the webs were built exclusively in soft rushes (*J. effusus*), and another 19% were built in rushes together with another species of plant. Most other plant species (e.g., burreeds, woolgrass, grasses) that were used by females for nursery webs were similar to *Juncus,* with linear, grasslike leaves. While shrubs and herbs such as lizardtail (*S. cernuus*) and smartweed (*P. hydropiperoides*) are plentiful at the pond's perimeter, they were rarely used for nursery webs.

DISCUSSION

We have found evidence in the fishing spider for an age-related switch in movement pattern. Juveniles clearly employ a sedentary strategy throughout much of the year. Following their last molt, newly-adult females switch to an active period characterized by frequent movement. Presumably, increased movement by spiders also increases their exposure to predators (e.g., Vollrath 1985). Increased movement also incurs a greater metabolic cost. Studies with wolf spiders show that active metabolic rates are *ca.* 3–4.5× resting rates (Miyashita 1969; Ford 1977; McQueen 1980). Thus, metabolic costs may play a significant role in foraging decisions by cursorial spiders, especially when coupled with the likely increase in predation risk. These costs must be offset by benefits in order for increased movement to be an adaptive behavioral option.

Norberg (1977) was among the first to ap-

ply optimal foraging theory to the selection of foraging modes. He contrasts a foraging mode with a high feeding efficiency but high energetic costs (mobile strategy) to one in which both feeding efficiency and costs are low (sit-and-wait strategy). Norberg's model minimizes daily foraging time, and predicts that predators should switch from high-efficiency, high-cost modes to low-efficiency, low-cost modes as prey densities, and thus energy resources, decline. While one of the most frequently observed shifts in foraging mode is indeed prey-density dependent, it is often in the opposite direction from Norberg's predictions. Many species switch from ambushing at high prey densities to active searching at low prey densities (e.g., diving beetle, Formanowicz 1982; water scavenger beetle larvae, Formanowicz et al. 1982; centipedes, Formanowicz & Bradley 1987; odonate larvae, Johnson & Crowley 1980; salamander, Jaeger & Barnard 1981). Helfman (1990) notes that each of these apparent contradictions to Norberg's predictions are ectothermic animals. He proposes that ectotherms, with relatively low metabolic needs and costs of activity, may behave to maintain a minimum encounter rate with prey. Endotherms, with higher metabolic energy requirements, may behave to maximize the ratio of energetic return to expense as Norberg's model predicts.

Formanowicz & Bradley (1987) argue that a more active strategy is utilized to increase the probability of finding prey when a predator has the greatest need to acquire energy, irrespective of cost. Support for this comes from studies which have shown hunger to be important in the foraging movements of a mantid (Inoue & Matsura 1983) and ant-lion larvae (Griffiths 1980). Both of these invertebrate predators employ an ambush strategy for prey capture, making frequent site changes as hunger increases. As Helfman (1990) points out, this situation is analogous to traditional optimal diet-selection models (e.g., Krebs & McCleery 1984), which predict a decline in prey selectivity as prey densities decrease. In both cases, predators are willing to expend more energy for an increased probability of successful intake of energy, while avoiding cheaper alternatives that entail a greater probability of failure.

It is likely that during the period between the last molt and egg sac formation, the en-

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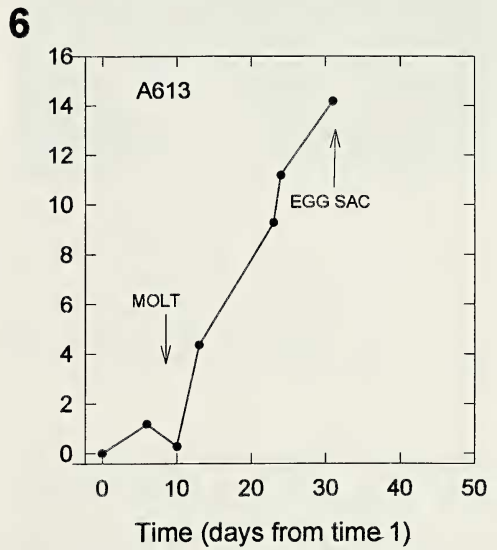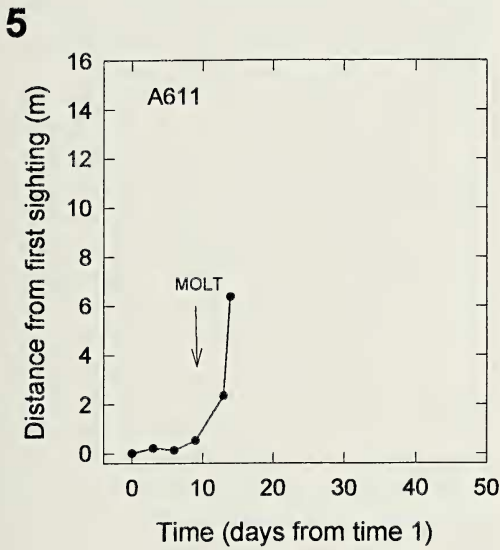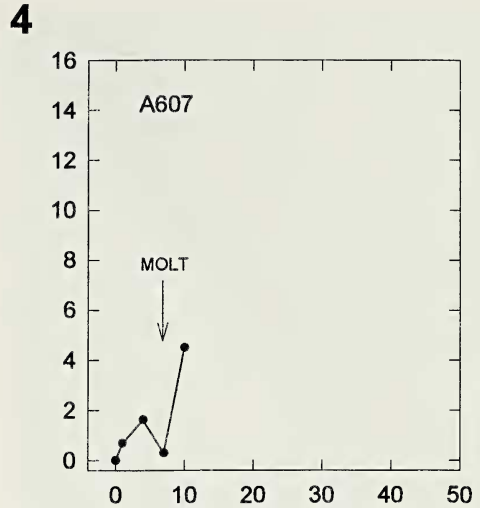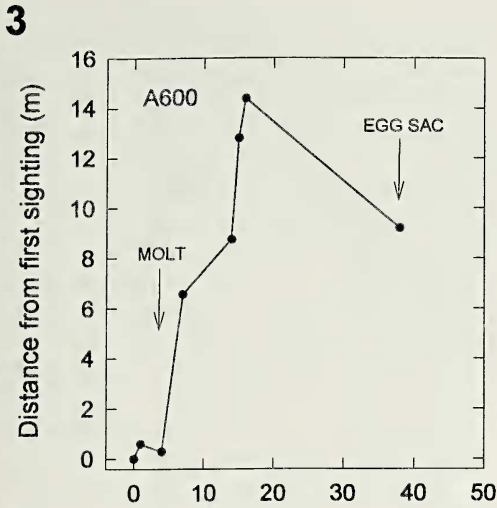
Figures 3–6.—The distance (in meters) from the first sighting for the four adult females for which data is available at least five days prior to the molt to adulthood.

ergy demands in adult female *D. triton* greatly increase, due largely to the accumulation of yolk in the eggs. Generally, yolk accumulation in spiders occurs in two steps (Seitz 1971, as cited in Foelix 1982). At first, fine-grained yolk particles aggregate in the young egg cell. After copulation, a second accumulation of yolk begins, this time in the form of much larger granules. In the cursorial spider *Cupiennius salei* Keys, egg cells increase ten- to twelve-fold in size during yolk accumulation, and the female's abdomen visibly swells. This second phase can take place only if enough food is available (Foelix 1982). Zimmerman

& Spence (1989, 1992) note that female *D. triton* feed intensively and are extremely cannibalistic following mating. Pronounced abdominal swelling during this period is evident in *D. triton* as well (see Figs. 7, 8).

The period of yolk accumulation is a time when foraging returns are extremely important. Field experiments supplementing the food of other species of female spiders have demonstrated that additional food results in increased fecundity (e.g., Wise 1975, 1979; Spiller 1984; see Wise 1993 for a review). Little information is available on the degree of food limitation in *D. triton*, but it seems likely
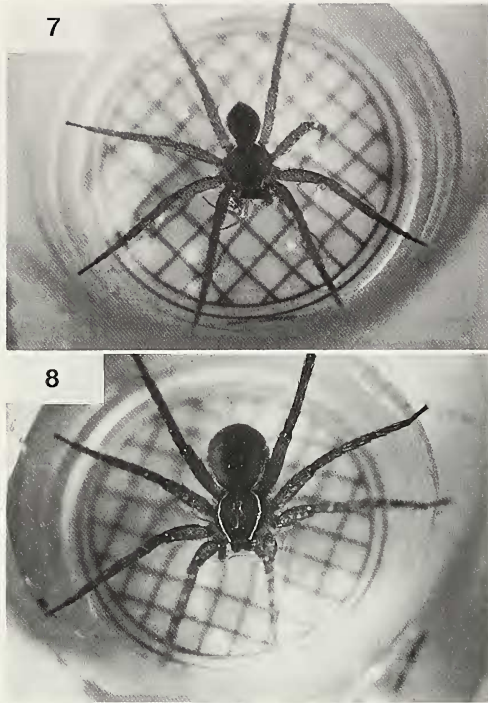
Figures 7–8.—Two adult female *Dolomedes triton* with similar carapace widths. The difference in abdominal size is notable. The female in the top photograph recently shed and has just begun yolk accumulation in the eggs, while the female in the bottom photograph is near the time of egg-sac construction.

that increased energy demands play an important role in its foraging strategy during the period of yolk production.

Why don't juveniles adopt a more active strategy for foraging? Food limitation of juveniles may have delayed effects upon fecundity, possibly due to a decreased capacity to carry eggs. For example, Schoener (1971) argues that increased food intake can affect reproductive output not only directly through size or number of eggs, but also by increasing the size of the parent, particularly when egg number is directly proportional to body size. Supplementing prey of juvenile spiders in natural populations has been demonstrated to result in increased growth (Wise 1975, 1983), and a strong correlation has also been found between size at maturity and egg production in spiders (e.g., Petersen 1950; Wise 1976; Wise & Wagner 1992). Thus, securing additional food during the juvenile stages should increase potential fecundity. Nevertheless, the

sit-and-wait foraging style of juvenile *D. triton* is closer to what Riechert & Luczak (1982) predict for spiders minimizing energy expenditure. One possible explanation for this comes from simple prey-encounter models (DeVita et al. 1982) which predict limited benefit from an active foraging strategy if the prey are small and fast species. It is not known, though, whether the strategy of the juveniles is due to the type of prey sought, or whether the prey type captured are a result of a sedentary foraging strategy.

Increased food acquisition is not the exclusive tenable hypothesis for the observed age-related difference in movement. Two alternative hypotheses are (1) evaluation of sites for egg-sac construction and nursery-web placement, and (2) differential predation pressures. The preference we found for placing the nursery web in *J. effusus* suggests that the site of egg construction is not random. As noted above, female *D. triton* carrying egg sacs move very little, spending approximately 3–4 weeks without food as they tend their egg sac. Once the egg sac begins to hatch, the nursery web is placed in the vegetation in the immediate vicinity. Selection of a site for the nursery web must therefore take place prior to sac construction. Aside from the structural properties of the vegetation, other features which may be important include predatory risks, density of conspecifics, and abiotic factors (e.g., temperature, humidity, the presence of wind-generated waves). Although these features may play a role in the final selection of a site, they are unlikely to be determining factors in the observed increase in activity of adult females. If the movement is driven by a search for an appropriate site, females would be expected to encounter appropriate sites at random periods of time following mating. Thus, some females should locate superior sites the day after their last molt, after which they should stop moving and thereby conserve energy, particularly if superior sites are limited. This pattern was not observed in the field during 1991 and 1992. Rather, females continued to move until egg-sac construction.

Differential predation pressures on adults and juveniles could play a role in causing the different movement patterns of the two ages, although rates of mortality from predation are not known for *D. triton*. Predation by fish during 1991 and 1992 was documented several

times as individuals moved across open water. An instance was reported by Carico (1973) in which a number of *D. triton* were found in the gut of an immature little blue heron (*Florida caerulea*), a species known to use a visual hunting style. Roble (1985) reports predation on *D. triton* by pompilid wasps, which also hunt visually. Great blue herons (*Ardea herodias*) were commonly seen hunting along the shores in the ponds at our study sites, but pompilid wasps have not been observed. Juvenile and adult female spiders are probably equally subject to predation by vertebrate predators such as wading birds, fish and frogs. However, the increased size of the adult females might make them less likely to be prey of other invertebrate predators of the pond. The risk of cannibalism is also probably higher for the juvenile age class. The switch to increased movement is not gradual, though, as might be expected if release from predation pressures due to size were solely responsible. Instead, the change from sedentary to active foraging takes place only after the final molt. Furthermore, the fact that juveniles remain stationary through August, September, and at least part of October, when few adult females remain on the pond, suggests that juveniles are averse to movement even in the absence of a potential major predator.

In summary, an age-related switch in movement patterns was observed in *D. triton*. It is argued that this switch represents a change in the foraging mode of adult females from sit-and-wait to active forager. It is hypothesized that this change occurs because the active mode provides a higher rate of energy gain, which is needed to meet the increased energy requirements of yolk production. Although an active strategy is metabolically more costly and results in increased exposure to predators, it may be necessary to ensure enough energy for egg production.

ACKNOWLEDGMENTS

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